FINAL MANUSCRIPT

Title: Causes of the Cambrian Explosion

Authors: M. Paul Smith[1]* and David A.T. Harper[2]

Affiliations:

[1]Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK.

[2]Department of Earth Sciences, Durham University, Durham DH1 3LE, UK.

Correspondence to: paul.smith@oum.ox.ac.uk

Main text:

In the last decade, at least thirty individual hypotheses have been invoked to explain the Cambrian Explosion, ranging from starbursts in the Milky Way to intrinsic genomic reorganization and developmental patterning. It has been noted (*1*) that recent hypotheses fall into three categories: a) developmental/genetic, b) ecologic and c) abiotic environmental, with geochemical hypotheses forming an abundant and distinctive subset of the last. With a few notable exceptions, a significant majority of these hypotheses have been posited as stand-alone processes that constituted the principal causal modes of the Explosion. An additional challenge relates to the precise definition of the Explosion – is it the first appearance of animal groups, the diversification event, the emergence of marine ecosystems with 'modern' trophic structures, or all of these?

Debate over the temporal pattern of diversification has now reached a position of some stability, with a clear distinction between the first appearances of high-level animal crown-groups in the Neoproterozoic, and then in the early Cambrian the main diversification of animal groups, a significant increase in morphological disparity and the emergence of complex food webs (*2-4*). The molecular clock estimates, using housekeeping genes, predict that the origins of the metazoan crown-group, together with the demosponge, cnidarian and bilaterian crown-groups, lie deep in the Cryogenian period (850–635 Ma), whereas the first appearance of over 100 extant phyla and classes occurs within the Cambrian and only a handful predate the base of the Cambrian at 541 Ma. Two inter-related events are thus distinguishable, with the origin of high-level animal groups temporally distant to the abrupt increase in diversity and disparity within the Cambrian – the Cambrian Explosion *sensu stricto*.

The advent of bilaterian developmental systems is an integral part of the Cambrian Explosion and it has been argued, for example, that the principal cause of the event is the origin of the bilaterian gut and macrophagy in the late Cryogenian, at around 650 Ma, which in turn enabled the evolution of large body sizes and skeletons in response to benthic predation pressures (*5*). This ignores, however, an apparent >100 million year gap between the evolutionary innovation and its downstream consequences. Whilst developmental systems must be in place to enable the macroevolutionary cascade, the smoking gun(s) of the Cambrian diversification must lie closer to 540 Ma than 650 Ma. Whatever the trigger was, stem-bilaterians had already evolved the developmental toolkit to exploit the complex mosaic of opportunities that arose (*6*).

With macrophagy in place, the emergence of complex food webs is then a significant intrinsic driver for diversity increase in the Cambrian Explosion (*1, 7*), partly because of the ecosystem engineering of substrates (*8*) but also because the inherent 'evolvability' of metazoans, and their tendency to induce arms races, may account for much extant diversity (*7*). This type of feedback is manifest in the origins of plankton/nekton, burrowing and biomineralization, which initially are *de novo* evolutionary products but then contribute a series of additional feedback loops that accelerated the evolutionary cascade and diversification. In the case of biomineralization, this is manifest in the near simultaneous appearance of both predatory and defensive hard tissues across a wide range of animal groups predominantly utilizing two separate calcium biomineral groups, the carbonate isomers and apatite (*9, 10*). Although it has been argued that the emergence of complex food webs is the result of crossing a threshold or tipping point (*7*), it is equally likely that this is a downstream, distal result of complex feedback loops (see figure).

Recently, attention has returned to abiotic processes as a possible activator of the Explosion, with the proposal that the flooding of hyper-eroded, peneplaned continents in the early, but not earliest, Cambrian triggered a range of Earth system responses (*11*) including enhanced weathering of both regolith and crystalline rock and the rapid input of a range of ions into oceans, including Ca^{2+} (*11*) and PO_4^{3-} (*12, 13*). Calcium concentrations reached a Phanerozoic high in the Cambrian and this input may have directly facilitated the origin of biocalcification (*14*), whereas the input of phosphate provided significant nutrient input to shallow-water areas (*12, 13*).

Each one of the hypotheses outlined here is a viable trigger for increases in α-diversity (mean species diversity with habitat), β-diversity (differentiation between habitats) or γ-diversity (total regional biodiversity). The key, however, to elucidating the explosive increase in diversity is likely to lie not in the selection of any one favored hypothesis but, rather, in understanding the connectivity and co-dependencies of the individual hypotheses. The causes of rapid diversification in the early Cambrian are thus unlikely to be reliant on a single mechanism and many of the individual hypotheses proposed over the past ten years, and earlier, are probably components of interacting feedback loops between Earth systems and biological processes. Together, ignited by an initial trigger, these generated the evolutionary cascade that led to the rapid rise in diversity. It may be more valuable, therefore, to model the event more holistically, removing the need to identify just one causal factor. Distinguishing between proximal and distal, upstream and downstream causal factors within the c. 25 million year duration of the event will provide a more realistic framework for understanding this unique event in Earth history.

That initial trigger is likely to have been the early Cambrian sea-level rise that led to inundation of continental margins and interiors and a rapid input of erosion by-products (*11*). Simultaneously, the sea-level rise would have generated a large increase in habitable area lying between normal wave base and the base of the photic zone, in turn providing a driver for large increases in diversity and habitat partitioning.   These factors segue into the complex interaction of abiotic and biotic processes, emphasizing that there is no one single 'cause' of the dramatic increase in diversity and disparity in the early Cambrian carnival of the animals.

References:

1. C. R. Marshall, *Ann. Rev. Earth Planet Sci.* **34**, 355 (2006).

2. D. H. Erwin *et al.*, *Science* **334**, 1091 (2011).

3. *The Cambrian Explosion: the construction of animal diversity*, D. H. Erwin, J. W. Valentine, (Roberts & Co., Greenwood Village, CO, 2013), 406 pp.

4. C. J. Lowe, *Science* **340**, 1170 (2013).

5. K. J. Peterson, M. A. McPeek, D. A. D. Evans, *Paleobiology* **31** (2, Suppl.), 36 (2005).

6. D. H. Erwin, E. H. Davidson, *Development* **129**, 3021 (2002).

7. N. J. Butterfield, *Trends Ecol. Evol.* **26**, 81 (2011).

8. R. H. T. Callow, M. D. Brasier, *Earth Sci. Rev.* **96**, 207 (2009).

9. D. J. E. Murdock, P. C. J. Donoghue, *Cells Tissues Organs* **194**, 98 (2011).

10. R. Wood, A. Y. Zhuravlev, *Earth Sci. Rev.* **115**, 249 (2012).

11. S. E. Peters, R. R. Gaines, *Nature* **484**, 363 (2012).

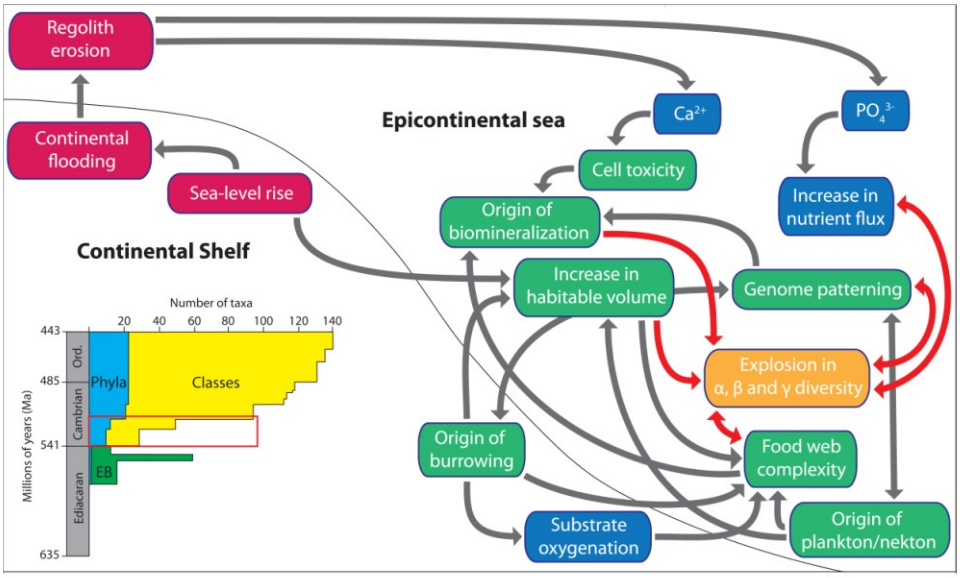
12. P. J. Cook, J. H. Shergold, *Nature* **308**, 231 (1984).

13. M. D. Brasier, R. H. T. Callow, *Mem. Ass. Austral. Palaeont.* **34**, 377 (2007).

14. S. T. Brennan, T. K. Lowenstein, J. Horita, *Geology* **32**, 473 (2004).

Figure caption

A range of phenomena associated with the major diversification of marine taxa early in the Cambrian have been hypothesized as isolated, singular causes of the event, but in most cases sit within a series of cascading and nested feedback loops that unite a range of Earth system, developmental and ecological processes. Each box corresponds broadly to a stand-alone hypothesis or suite of related hypotheses; red indicates predominantly geological processes; blue, geochemical; and green, biological. The figure represents a narrow interval of time at the base of the Cambrian (541–521 million years ago). The inset chart shows the major diversification of marine taxa at high taxonomic levels from 635–443 Ma (after Erwin *et al.*, *2*), and the red box indicates the time interval discussed in the text (EB, Ediacaran Biota).



Regolith erosion
Continental flooding
Sea-level rise
Continental Shelf
Epicontinental sea
Ca^{2+}
PO_4^{3-}
Cell toxicity
Origin of biomineralization
Increase in nutrient flux
Increase in habitable volume
Genome patterning
Explosion in α, β and γ diversity
Origin of burrowing
Food web complexity
Substrate oxygenation
Origin of plankton/nekton
Number of taxa
20
40
60
80
100
120
140
443
485
541
635
Ord.
Cambrian
Ediacaran
Millions of years (Ma)
Phyla
Classes
EB